



THEESIS

RUST OF ANTIRRHINUM

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Rust of *Antirrhinum*.

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I. INTRODUCTION

The cultivated snapdragon (Antirrhinum majus L.) is a perennial or biennial under culture. It is a member of the family Scrophulariaceae. The plant was introduced here from Europe. As an escape from gardens, it is rare in New England. The snapdragon has been a popular garden flower for two hundred years, but it is only within the last ten years that it has been grown to any extent as a greenhouse crop. There has been an increasing demand for it as a cut flower, and consequently an increasing amount of glass has been devoted to its culture. As a florist's crop, the snapdragon may be classed as about equal in importance to mignonette, schizanthus, stocks, pansies, and primulas (Nehrlin, 1914), varying, of course, in different localities.

The high prices paid induced the growers to propagate for the best colored blossoms and the best formed spikes, and only slight attention was paid to the susceptibility of the plants to disease. Increased and intensive cultivation seems to have weakened this once hardy plant, for it is now affected severely by at least three fungous diseases and one physiological disease. The diseases of snapdragon other than the rust, are anthracnose or leaf spot, caused by Colletotrichum antirrhini Stewart, stem rot caused by Thoma sp. and a physiological trouble characterized by a curling and puckering of the leaves. A septoria disease occurs on snapdragon in Europe but not in this country. Rust is the most serious of the snapdragon diseases under glass, but, according to the observation of the writer, anthracnose is a more serious disease than rust on plants grown outdoors. The stem rot and anthracnose of snapdragons are

described by Stewart, (1900). Investigation of this rust has been undertaken because of the economic importance of the disease, and because there was so little information concerning it available to the growers. Rust causes loss in at least three ways. A spike of snapdragons blossoms is useful only when it is beautiful, and the rust pustules on leaves and stems considerably mar the appearance, and hence lessen the value of otherwise salable spikes. An attack of rust impairs the vitality of the host plant, and results in smaller flowers and shorter spikes than the normal. In severe cases, the stems and branches are girdled, causing the death of the plant. No figures are available as to the actual monetary loss caused by this disease.

II. HISTORY AND DISTRIBUTION

This disease was found in California in 1897 (Dietel 1897). In 1913, it appeared in Illinois, and in 1914 it was found in Ohio and Indiana (Rees 1914). By 1915, the rust was well established in New England, both out of doors and under glass. The writer has seen the disease in Maine, New Hampshire, Massachusetts, Rhode Island and Connecticut. In 1916, it was reported from Guelph and Montreal, Canada. Apparently, snapdragons rust is very generally distributed over the Northern part of the United States wherever the plant is forced for commercial purposes. Apparently it does not occur in the British Isles nor on the continent of Europe. (Letter to the writer from Mr. F. Chittenden of the Royal Horticultural Society's Staff, 1915).

(1) ACYNOAL DGM. T. The writer wishes to express his appreciation for helpful suggestions and criticisms received from Prof. A. V. Osmun, of Massachusetts Agricultural College and Dr. C. R. Butler of New Hampshire Agricultural Experiment Station, under whose direction the work was carried on.

III. SYMPTOMS

Snapdragons may occur on plants of all ages, from seedlings just beginning to show foliage leaves up to mature blossoming plants. A severely attacked snapdragon has a most dejected appearance; the leaves hang limp and wilted as if the plant had been deprived of water, the flowers open small and prematurely and leaves and stems bear chocolate-brown powdery pustules, each edged by a yellowish ring. Leaf blades, petioles, stems, and calyxes are attacked. In the early stages on the under side of the leaves appear swollen yellow patches just inside the epidermis. These yellow patches are 1-7 mm. in diameter. At this time, the leaf may curl slightly. About forty-eight hours after these yellowish patches first appear, the epidermis is ruptured exposing brown powdery masses beneath. These uredosori, as the brown masses are called, have been described as being usually circularly grouped (Clinton 1915), but according to the writer's observation, circular grouping is not a dependable characteristic. On the upper surface of the affected leaves are yellow blotches, corresponding in position to the uredosori beneath. The spore powder in the uredosori is in an agglutinate condition, at first, but after a few days, it becomes dry and dusty and easily blown about.

The ring of ruptured epidermis surrounding a uredosorus is soon concealed by this brown spore powder. Usually the lower leaves of the plant are most affected. The sori on the stem are much elongated. Here, the ruptured epidermis is more noticeable than on the leaves. Sori on the stem usually occur at the base of a petiole or at the crotch of two branches or any place where water may stand. These sori sometimes girdle the stem, in which case the plant wilts or dies. It is not especially common, however, for snapdragon rust to cause the death of the host plant. The telcosori are black, not brown. They

are leathery, not powdery, and must be scraped off if they are to be removed. They are considerably more common on the stems than on the leaves but are not numerous anywhere.

The disease occurs at all seasons of the year but is most serious and most conspicuous in the greenhouse during April and May.

IV. CAUSAL ORGANISM

1. Morphology

Snapdragon rust is caused by the fungus Puccinia antirrhini Diet. & Holw. It was named by Dietel (1897) from material collected by Blasdale at Berkeley, California. Two types of spores are known in the life cycle of the fungus; viz., urediniospores and teliospores.

(a). Mycelium

The mycelium of the fungus occurs chiefly between the spongy parenchyma cells of the leaf and between the cortex cells of the stem. It is more abundant in the leaf than in the stem. It is colorless, septate and branches profusely. It is intercellular and provided with haustoria (Fig. 4 Plate 2.) The haustoria are constricted at the point of entrance to the cell. Within, they become broader and vase shaped or bear short knob-like branches. A dilute solution of eosin makes the haustoria easily visible.

(b). Urediniospore stage.

A cross section through an infected leaf reveals beneath each sorus a stroma of interwoven mycelium. (Figs. 1 and 5. Plate 2.) This stroma underlies the whole sorus and extends in a ring around its edge. From this stroma, the spore bearing hyphae arise. The urediniospores are spherical to elliptical. They are 22 to 30 microns in length, and 21 to 25 microns in diameter. They are borne on pedicels of varying length from which they become detached at maturity. The urediniospores are light brown in color. Their walls are provided with short spines.

The uredinia are chocolate brown in color, never black. They are not sunken. They are confluent with age.

(c). Teliospore stage.

The teliospores are 36 to 50 microns in length and 17 to 26 microns in diameter. These spores vary greatly in shape. (Fig. 2, Plate 2.) The apex may be sharply pointed, rounded, or truncate; the base is usually attenuated but may be rounded off bluntly. There is a slight constriction at the septum. The epispires are dark brown to black, and the wall is smooth, possessing no such spines as occur on the uredospores. Each of the two cells of the teliospore is provided with a germ pore, which is apical in the terminal cell, and occurs just below the septum in the basal cell. The telia are black and hard or leathery. They are slightly smaller than the uredinia. They occur more frequently on the stem than on the leaves, and are usually somewhat sunken, with the ruptured cuticle projecting above them. The teliospores are sometimes borne in the same sorus as the urediniospores, but the telia may be distinguished macroscopically by their blacker upper rame and harder structure.

2. Occurrence of Spore Stages.

Urediniospores occur at all times on the diseased snapdragons. In the greenhouse, these are normally the only type of spores produced. Teliospores occur only rarely in New England. Many infected plants bear only urediniospores, even on the advent of killing frosts. Occasionally, teliospores may be found outdoors in November, occurring more often on the stems than on the leaves. In November, the writer placed snapdragons bearing uredinia in wire baskets, and allowed them to winter over out of doors in this way. Examination the following March showed only one telium on all the material.

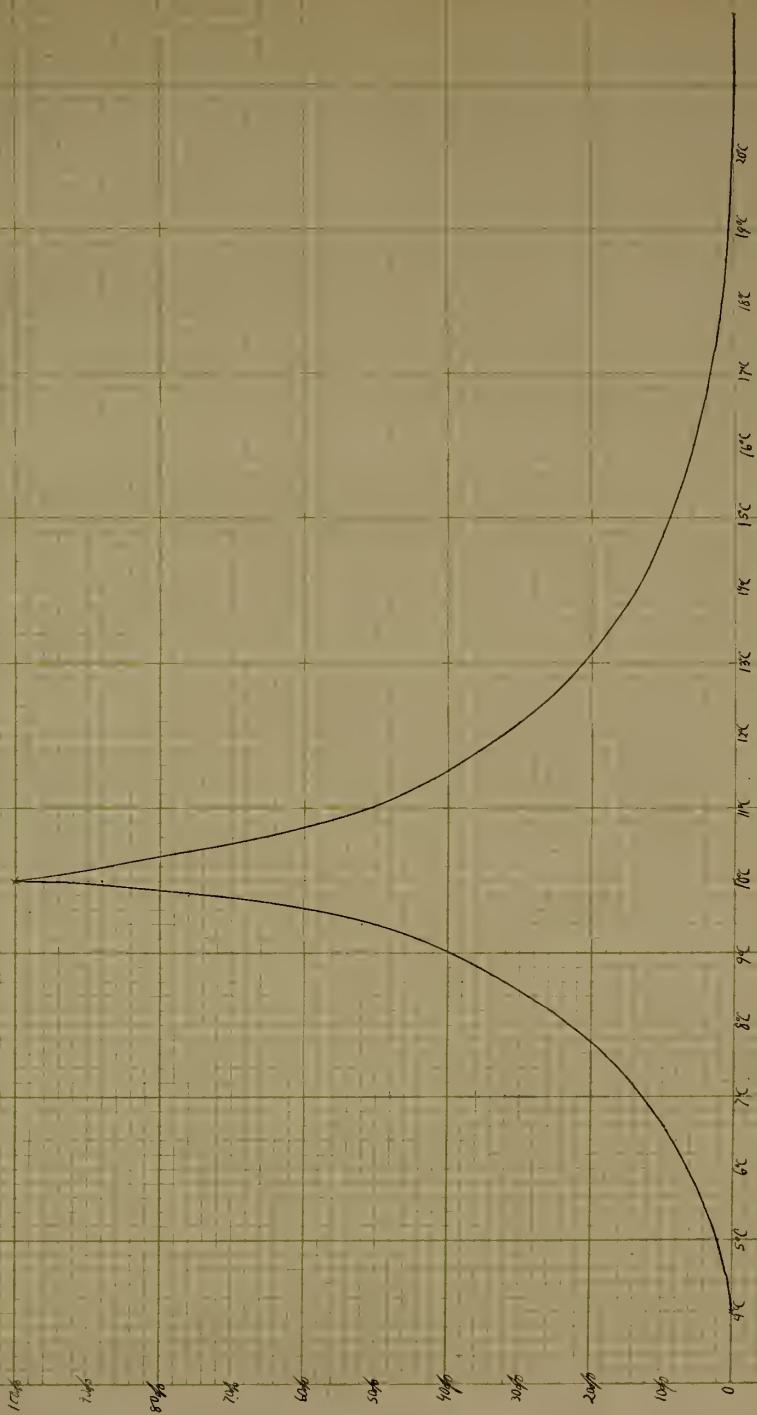
In the greenhouse there is no lowering of temperature to stimulate the formation of teliospores. But their formation is stimulated if the host plant dries out very slowly. If the plants are suddenly dried out, no teliospores are formed, but when greenhouse plants were very gradually deprived of water, teliospores were formed in five weeks. Under normal conditions of culture, we may eliminate the teliospore as a factor in the greenhouse. No greenhouse snapdragons seen by the writer showed teliospores except those plants upon which this part of the experiment was performed.

3. Spore Germination and Infection Experiments.

(a) Temperature relations.

The first attempts made to germinate these spores were not uniformly successful. As it proved later, this was because the room temperature was above their maximum temperature for germination. The method by which the minimum, optimum, and maximum temperatures for the germination of these spores was determined is here described.

The spores used were removed from infected leaves by a stream of water from a pipette. In this way, only mature spores were obtained, while scraping with a brush or wooden instrument would also detach young, immature spores. The spores were shaken in distilled water until they were uniformly distributed through it. Drops of this water containing the spores were then placed on clean slides, and the latter were placed on culture plate benches in moist chambers. These were then placed in biological incubators at constant temperatures. About twelve hours later, the germinated and ungerminated spores were counted. Most of the spores germinated, however, in five to eight hours. Throughout these tests it was noticeable that no spores in the interior of the drop ever germinated. Only those spores in contact with the air as well as the water germinated, so spores in the interior of



Spore Germination - Temperature Curve

the drop were not counted as present. This aerotropism was not further investigated. Throughout the tests, one lot of spores was always run at 10 degrees C. The percentage of germination at 10 degrees C was taken as a standard, raised to 100, and the other percentages at the different temperatures raised proportionately. This was done in order to bring the data into shape for plotting a constant curve of temperature and germination.

The optimum temperature for the germination of the urediniospores of *I. Antirrhini* was found to be 10 degrees C., the minimum 5 degrees C., and the maximum 20 degrees C. When the data is plotted, a curve is obtained that is nearly symmetrical. A most striking fact is that if the temperature is varied two degrees C. above or below the optimum, the germination falls off 50 per cent. In the following table each relative germination is the mean of five experiments.

TABLE 1. Relative Germination of Urediniospores of *Iuccinia antirrhini* compared to the Germination at 10 degrees C. taken as 100.

5°C.	6°C.	7°C.	8°C.	9°C.	10°C.	11°C.	12°C.	14°C.	15°C.	18°C.	20°C.	30°C.
0	0	27	13	50	100	145	21	0	17.5	2.5	0	0
0	0	0	35	30	100	42	15	12	13	0	0	0
1	4	7	37	50	100	9	32	0	0	0	1	0
0	0		4	12	100	14	16	42	6	1.5	0	0
1	4		21	30	100	72		2	1	1	0	0
0	3			100			22		.5	0	0	
0	0			100					1	0	0	
0	2			100					0	0	0	

(b) Conditions Affecting Longevity of Urediniospores.

The spores used in the previously described germination tests were taken fresh from growing plants in most cases. It was noticeable

that their viability gradually diminished if the leaves dried out long in the room. To determine the longevity of urediniospores, rusted shoots were removed from the plants and placed at temperatures of 10°6, 22°0, and 0°0C. Half of this material was allowed to dry in open boxes and half of it was placed in closed vessels to prevent its drying out. Spores were removed every seven days and placed at their optimum for germination.

TABLE 2. Effect of Temperature and drying on the longevity of the Urediniospores of *I. antirrhini*.

Storage Temper- ature	Germination of Uredospores at end of															
	7 days.		14 days.		21 days.		28 days.		35 days.		42 days.		49 days.		56 days.	
	Dry	Moist	Dry	Moist	Dry	Moist	Dry	Moist	Dry	Moist	Dry	Moist	Dry	Moist	Dry	Moist
	Air	Air	Air	Air	Air	Air	Air	Air	Air	Air	Air	Air	Air	Air	Air	Air
	Per cent	Per Cent	Per cent	Per cent	Per cent	Per cent	Per cent	Per cent	Per cent	Per cent	Per cent	Per cent	Per cent	Per cent	Per cent	Per cent
0°0C	55	52	35	35	20	18	12	18	1	10	0	3	0	1	0	0
10°0C	50	52	25	20	20	12	15	15	2	6	0	2	0	1	0	0
22°0C	40	50	28	25	15	20	12	15	3	5	0.5	2	0	0	0	0

hen this experiment was begun about 60 per cent of the spores germinated. After remaining 42 days in dry air no spores germinated. Spores in moist air retained the power of germination 49 days. Exposure to freezing temperatures does not shorten the life of uredospores. In southern New England and southward the snapdragon remains green throughout the winter if slightly protected by a straw mulch. In January, the writer obtained urediniospores from green plants growing outdoors. These uredospores germinated. But after the plants had been dried three weeks at room temperature, the spores no longer germinated. Temperature is of less importance than drying in shortening the life of urediniospores.

(c). Effect of Temperature on Infection.

Twelve plants were sprayed with fresh spores in distilled water. Four plants were placed at a temperature of 10°0C, four at 15°0C, and four at 18°0C. The plants used were a susceptible variety, Carter's Link, but they were free from disease when selected. The plants re-

mained in the above-mentioned temperatures twelve hours, after which they were all placed in the greenhouse at the same temperature. Seven days later the stromata were visible. Ten days after inoculation, the uredinia began to appear. One week later the number of sori on the plants was counted.

TABLE 3. Effect of Temperature on the Infection Lower of the Urediniospores of *L. antirrhini*

Plants inoculated at	Number of Sori per Plant				Mean Infection in Relative Numbers
10°C.	240	265	210	180	100.0
15°C.	9	6	15	20	7.6
18°C.	5	3	7	9	3.5

Raising the temperature 5 to 8 degrees above the optimum for germination of the fungus causes the amount of infection to fall off more than 90%.

As a further test of the effect of temperature on infection of snapdragons by Fuccinia antirrhini, plants of a susceptible variety were inoculated in two different greenhouses, having a night temperature of 10°C. in one case, and 15°C. in the other. Fifteen days after inoculation, the plants in the greenhouse at 15°C. bore an average number of 12 uredinia. At the same time, the plants in the house at 10°C. were only 10, as badly rusted as the plants in the house at 50 degrees F.

As indicated by the results with *L. antirrhini*, the rusts are able to germinate best at rather low temperatures. A consideration of the literature also supports this view. Erikson (1895) discovered that low temperatures are suitable to the germination of rust spores. He found that the spores of Aecidium Berberidis germinate best when cooled for seven hours to 3°C., and that the spores of Leridermium

strobi germinated best when cooled for twenty-four hours at 6.5°C. He found the optimum temperature of Uredo glumarum to be 4.5°C, and he found that the spores of Uredo coronata germinated best after being cooled for sixteen hours to a temperature of - 10°C. In the last case, it seems probable that he went below the optimum temperature and that the spores germinated when the temperature again rose to the optimum.

Howell (1890) found that the urediniospores of Uromyces Trifolii (Alb. and Schw.) sint. germinate best between 11 and 16 degrees C. They do not germinate below 7 degrees C. nor above 21 to 25 degrees C. If the minimum, optimum, and maximum temperatures for germination of Uromyces Trifolii are taken as 7°, 11°, and 21° respectively, this fungus has about the same temperature-germination relation as does Luccinia antirrhini, the minimum, optimum, and maximum temperatures for germination of uredospores of L. antirrhini having been found to be 5°, 10°, and 20°C. respectively.

(d) Experiments on germination of teliospores.

Numerous attempts to germinate teliospores were made with fresh material, dried material, teliospores produced under glass, teliospores produced outside and teliospores wintered over outside. These germination tests were made at 7°C, 10°C, 12°C, and 20°C, but in no case did the teliospores germinate. These spores had formed in response to the definite stimulus of cold or of drying. They do not germinate when first formed; they are spores of regeneration and they may be considered as requiring a rest period, like other spores which function to carry fungi through adverse conditions. But these teliospores did not germinate after the rest period, that is, after passing the winter out of doors, when subjected to the range of temperature in which their host normally grows. It is probable that they were

illed by the cold, not being able to withstand the rigors of the winters to which their host has been carried.

The fact that teliospores do not germinate may be explained in another way. The temperature-germination curve for urediniospores is very sharp, and if teliospores have an even narrower range of temperature through which they can germinate, it is possible that the right temperature for germination has not yet been hit upon, since a variation a few degrees above or below the optimum would result in no germination.

According to our present knowledge, the teliospores are not only rare but do not germinate. This being the case, the possibility of an alternate host is eliminated. But no alternate host is necessary for a fungus which passes the winter under glass. The chrysanthemum rust (Puccinia chrysanthemi Roze.) in America dispenses with both an alternate host and teliospores. Yet this rust occurs both in the green-house and out of doors and persists from year to year. The parasite is independent of the other rusts found on nearly related Compositae, just as Puccinia antirrhini is not a parasite on Linaris, a closely related genus in the family Scrophulariaceae. (Atkinson 1890). Carnation rust (Uromyces eucalyptillimus) has an alternate host (Euphorbia germiniana) in Europe. (Fischer 1910) but it has not been found on an alternate host in this country. If the teliospores of Puccinia antirrhini ever were functional, they seem now to be useless. The urediniospores of this fungus are sufficient to propagate it through the year, as long as greenhouses in the vicinity shelter the host plant during winter. The urediniospore is a spore of dissemination. Spores of regeneration, such as teliospores are not a necessity for a fungus the host of which occurs both under glass and out of doors.

(c) Experiments with *Linaria*

A theory has been advanced that snapdragon rust might be carried over from year to year on *Linaria vulgaris*. (Rees 1914). Observations and experiments of the writer indicate that *L. antirrhini* does not occur on *Linaria*. The writer examined *Linaria vulgaris* Hill. occurring in Massachusetts, Rhode Island, Connecticut and New Hampshire, but on one of these plants was this rust found. Attempts were made to infect *Linaria vulgaris* and also *Linaria Cymbalaria* (L.) Mill. with this rust from snapdragons. But these attempts were never successful on either species. Dr. Stone of the Ontario Agricultural College was unable to find the disease on *Linaria vulgaris*, or to infect this and two other species of *Linaria* with snapdragon rust.¹

5. Dissemination

(a) By cuttings

Snapdragon rust is at its height in March, April, and May. Many growers take their cuttings at that time. There are various opinions as to the relative merits of raising plants from seeds and from cuttings. But plants raised from cuttings are likely to come true to color, and in the effort to preserve a good variety, many growers take rust-free cuttings from a bench showing rust, or, worse still, they take cuttings bearing spore pustules. Some believe that if the cuttings show no spore pustules, they are safe to use, even though they come from an infected bench. The writer propagated plants by cuttings bearing uredosori and by cuttings bearing no sori, though taken from an infected bench. The result is shown in the following table.

1. Letter received from Dr. J. E. Stone, October, 1916.

TABLE 4. Dissemination of *Uuccinia antirrhini* by Cuttings.

Rust free cuttings from an infected bench.		
Variety.	Number of Cuttings made	Number of Cuttings rusted after three weeks
Delicate Rose	10	6
Giant Rose	10	4
Giant Scarlet	12	3
Crimson and Gold	10	2
Cuttings Bearing Sori when made		
Variety.	Number of Cuttings made	Number of Cuttings showing rust after three weeks
Giant Dark Scarlet	20	20
Hephaestos Red	20	20
Rosy Morn	24	24
Scarlet	20	20

It is evident that a cutting bearing spore pustules may be expected to develop into a rusted plant. And even cuttings free from spore pustules if taken from an infected bench serve to aid in the dissemination of the fungus. Microscopic examination of the leaf surfaces of these apparently healthy cuttings revealed numerous uredospores which had blown there from diseased plants. These spores need only the favorable conditions of the cutting bench to cause them to germinate and begin an infection. It is advisable to take cuttings from a house showing rust.

(b) Dissemination by Insects

Three insects often found on snapdragon are the white fly (Aleyrodes vaporarium), the red spider (Tetranychus telarius), and the common aphid (Aphis gossypii). With the binocular microscope, the writer examined these insects on snapdragon foliage. They happened to

be on healthy plants, but there were rusted plants in the same bench. On the bodies of nearly all these insects were the fresh and mature uredospores of Luccinia antirrhini. This in itself is sufficient proof of the importance of greenhouse insects in the spread of this disease. In passing it may be mentioned that the snapdragon is one of the most susceptible plants to the toxic effect of Hydrocyanic acid gas, and this important fumigant must be used with great caution, especially when the snapdragons are young.

(c) Dissemination by watering

Carnation growers no longer water overhead. They make an effort not to wet the foliage any more than is necessary, usually employing a long, stiff piece of hose or pipe which enables them to get water in the middle of the bench without wetting the plants above. This simple cultural method may be largely credited for the decline in importance of carnation rust. It is a hint to growers of snapdragons. The writer selected twenty snapdragon plants of the same variety all showing uredosori in approximately equal numbers. Ten of these plants were watered only on the soil, no water touching the foliage. The other ten were treated the same, except that their foliage was kept wet. After three weeks, the plants with wetted foliage showed 200% the number of uredosori they had at the beginning, while the plants, the foliage of which had been kept dry, showed no increase in the number of sori. Water is necessary for the germination of a spore and a germ tube does not enter a dry leaf. A careless stream from a hose loosens spores from a pustule, carries them to other plants, and provides them with the necessary moisture for germination. The snapdragon is native of a dry habitat; it will flourish on a rocky bank, and over-watering of the soil merely leads to an over-saturation of the atmosphere, and the increased moisture is usually followed by an increased number of infections.

Crowding the plants nearer together than 10 by 12 inches in the bench means that less light and air reaches the lower leaves, more water stands there, and more infections result.

V. PATHOLOGICAL ANATOMY

The upper epidermis of the leaf and the palisade cells are very rarely affected by this disease. Occasionally, a few palisade cells are forced apart by hyphae. The spongy parenchyma cells are, however, affected. These parenchyma cells in the immediate vicinity of a sorus do not attain their normal size. Strands of hyphae force them apart, and sometimes cause them to grow in abnormal forms. The chloroplasts fade slightly but the yellow appearance of the area surrounding a sorus is due mostly to the presence of a stroma of mycelium. After the intercellular mycelium has become well established, it develops this firm stroma in contact with the lower epidermis and often includes scattered spongy parenchyma cells. (See Fig. 5, Plate 2). This growing stroma and the rising pedicels of the uredospores finally rupture the epidermis. The contents of cells containing haustoria do not degenerate unless the whole leaf has become involved. Attacked cells do not swell, and any swelling on the leaf is due to the development of stromata. Leaf cells of snapdragons which are normally pink lose this pigment when attacked by the fungus. When the sori occur on the stem, the epidermis is ruptured, the cortical cells are forced apart, and in severe cases the mycelium may be found between the cells of the fibro-vascular bundles. Ordinarily, however, cells as far in as the phloem are not attacked. The chloroplasts fade even less in the stem than in the leaves. The cortex cells attacked do not attain their normal size. Epidermal cells appear unchanged, though raised as a membrane above a sorus. Mycelium in both leaf and stem is local.

VI. VARIETAL SUSCEPTIBILITY

Florists usually grow only a few varieties of snapdragon, such as Melrose, Silver Tink, Phelps White, etc. But gardeners who grow many varieties outdoors soon notice that some varieties are attacked by rust much more severely than are others. It has been recommended that only resistant varieties be grown, but there seems to be no list of resistant or susceptible varieties available. To learn what are the resistant and what are the susceptible varieties, the writer grew forty-seven varieties from seed. The seeds were obtained from A. T. Burlington of New York, R. & J. Farquhar & Co. of Boston, and Carter of London. This work was carried on in the winters of 1915-1916 and 1916-1917. The seeds germinated fairly uniformly if not planted too deeply, and when the potted plants had reached a height of about five inches, they were inoculated and placed under bell jars at 100° C.

Two weeks after the date of inoculation, the affected plants were examined and the number of rust pustules and affected leaves were counted. The diseased plants were examined at weekly intervals for the next five weeks, and observations recorded as to the number of rust pustules and affected leaves. In the following table of Relative Resistance, the most resistant varieties are named first, and the most susceptible are named last, the intermediate varieties being so arranged that any variety is more resistant than those which follow it. Varieties equally resistant or susceptible are connected by brackets. Each variety tested was represented by twelve or twenty individuals.

Since varietal names are not very well fixed, the color of the blossom and the height of the plant is given in most cases as an aid in identifying the varieties.

TABLE 5. Relative resistance of *Antirrhinum* Varieties to *Luccinia antirrhini*.

Variety Name	Color of Blossom	Height of Plant	Scale (Relative Numbers)
M (Queen of the North	white	2 Ft.	
))
P (Pure white	white	8 in.)
))
S (Rose Dore	Salmon rose	2 ft.)
))
T (Giant White	white	2 ft.)
))
) (Crimson	Crimson	2 ft.)
))
) (Giant Blood Red	Blood red	2 ft.)
))
R (Giant Yellow	Lemon yellow	2 ft.)
)			0
E (Striped Varieties	Variegated	2 ft.)
))
S (Hephnetos	Red and yellow	2 ft.)
))
I (Phelp's White	white	2 ft.)
))
S (Queen Victoria	White	2 ft.)
))
T (Queen Victoria	Crimson and gold	2 ft.)
A (Fire brand	Scarlet	15 to 18 in.)
))
N (Bridesmaid	White and pink	2 ft.)
))
T (Mont Blanc	white	18 in.)
Scarlet	Scarlet	15 to 18 in.	9
Giant Scarlet	Scarlet	2 ft.	16
(Half dwarf Defiance	Fiery scarlet	18 in.)
))
(Giant Garnet	Garnet	2 ft.)
)			23
(Giant Rose Pink	Rose pink	2 ft.)
Rosy Morn	Bright rose	15 to 18 in.	30
Giant Dark Scarlet	Dark scarlet	2 ft.	37
Half Dwarf Firebrand	Scarlet	12 to 15 in.	44

TABLE 5 (continued)

Variety Name	Color of Blossom	Height of Plant	Scale (Relative Numbers)
{ Nelrose	Bright silvery rose	2 ft.)
))
{ Silver Pink	Bright pink	2 ft.	(51
))
{ Carter's Butterfly	Crimson	2 ft.)
))
{ Orange King	Orange scarlet	15 to 18 in.	(58
))
{ Black Prince	Deep crimson	2 ft.)
))
Half Dwarf Daphne	Pink	15 to 18 in.	65
Bronze Queen	Red and white	15 to 18 in.	72
Deep Crimson	Deep crimson	2 ft.	79
{ Rose	Rosy pink	2 ft.)
))
{ Coral Red	Coral red	2 ft.	(86
))
{ Giant Pink	Pink	2 ft.)
))
Niobe	Crimson and white	15 to 18 in.	93
M { Half Dwarf Rose	Rose	15 to 18 in.)
O { Queen)
S { Fairy Queen	Orange and white	2 ft.)
T))
{ Ruby	Ruby red	15 to 18 in.)
))
{ Carter's Pink	Pink	2 ft.)
S))
U { Delicate Rose	Light rose	2 ft.)
S))
C { Half Dwarf Golden	Yellow	18 in.	(100
E) Queen)
P { Fiery Belt	Orange scarlet	2 ft.)
T))
I { Queen Victoria	Deep Crimson	2 ft.)
B))
L { Sulphur Yellow	Sulphur yellow	8 in.	(
E))
{ Venus	Pink and white	2 ft.)
))
{ Carter's Gold Crest	Pink and salmon	2 ft.	(
))
{ Chamois	Salmon pink	2 ft.)

This table shows that varietal resistance follows no rules of color of blossom or size of mature plant. Unfortunately the most valuable pink varieties such as Melrose and Silver Link are not at all resistant to the rust. The above table is perhaps of no great value to florists, for they must grow the varieties most in demand. But the table may be used as a basis in breeding resistant varieties, and is of some use to outdoor gardeners, for they can avoid the more susceptible varieties, and still have a satisfactory garden of snapdragons.

(a) Cause of resistance

Resistance of plants to disease has been explained in two general ways. Resistance may be regarded as being related with certain morphological characteristics. Cobb (1892) considered resistance to fungus disease as being due to small stomata, waxy coating, and thick cuticle on the host. Freeman (1911) found that increase in bloom on barley leaves made the plant more resistant to rust. Valleau (1915) studied resistance of plums to brown rot, and found resistance to be due to the production of parenchymatous plugs which fill the stomatal cavity and to lenticels composed of cork cells through which the hyphae cannot penetrate. On the other hand, resistance has often been regarded as due not to morphological characteristics but rather to physiological differences. Bille (1908) attributed resistance to chemical agencies such as toxins which arise as a result of the fungus attack upon the host. These few citations from the extensive literature on this subject illustrate the two views as to rust resistance.

The work done by the writer indicates that the resistance of some varieties of snapdragon to rust is due to morphological characteristics rather than to physiological differences.

The relative susceptibility of forty-eight different varieties of snapdragon to rust has already been given. The plants inoculated developed sori, some in large numbers, and some in small numbers. But

on both resistant and susceptible plants, the sori were developed in the same length of time, and there was no apparent difference in the vigor of the sori after they had once broken through the epidermis. This seems to indicate that the difference in susceptibility is not due to chemical factors within the host cell, but rather to mechanical factors preventing infection. The most susceptible plant is the one infected in the most places, that, the one into which the most germ tubes enter.

Infection is always through the stomata in the case of Luccinia antirrhini on snapdragon foliage. Urediniospores in distilled water were sprayed on living leaves, and eight hours later the leaf surfaces were examined microscopically. This was done repeatedly, but at no time was infection seen to occur anywhere except through the stomata. The plants used were placed in both light and darkness with stomata both open and closed. The germ tubes were protruded, wandered about slightly, and then bent into the nearest stoma, or, if the water on the leaf dried too soon, they shriveled up and never reached a stoma. But no germ tubes were seen penetrating the walls of the epidermal cells.

The mycelium within the leaf is local, therefore the number of sori on a leaf depends on the number of infections, and since infection is only through the stomata, it is interesting to determine the connection between the number of uredosori (the index of relative susceptibility) and the number of stomata.

Leaves were taken from three months old snapdragons of susceptible and resistant varieties. The number of stomata on the upper epidermis per unit area of leaf was counted. In each case, ten countings go to make up the average given for each variety. Ten susceptible

and ten resistant varieties were used.

TABLE 6. Relative Number of Stomata on Susceptible and Resistant Varieties of Snapdragons

Number of Stomata per Unit Area of Leaf.

Susceptible Varieties	Resistant Varieties
3.1 Stomata	1.5 Stomata
4.1	1.5
3.0	2.0
2.0	1.0
3.0	1.3
3.3	1.6
3.0	1.1
2.8	1.7
5.0	1.1
3.2	1.8

The averages of these figures show that there are 3.25 stomata on the susceptible varieties to 1.46 stomata on the resistant varieties. Or, stated differently, the resistant varieties have only 45 per cent as many stomata as do the susceptible varieties. The susceptible varieties showed approximately 100% as many uredinia as did the resistant varieties. This could indicate that susceptibility is directly proportional to the number of stomata. That is, doubling the number of stomata, doubles the number of uredosori or the amount of infection. However, such a relation is relative rather than absolute.

This explanation of resistance is not very different from Valleau's explanation of the resistance of plums to infection by the brown rot fungus. He found that the plum having the most unplugged stomata or unplugged lenticels was most susceptible, just as the snapdragon having the most stomata is most susceptible to infection by *Luccinia antirrhini*.

It may be added that the stomata on resistant and susceptible varieties are present in the same numerical relation if both upper and lower epidermis are considered. The figures in Table 2 are for

the upper epidermis only, secure owing to the fact that little or nothing clings to the lower epidermis, infection is mostly through the upper epidermis.

The stoma is the gateway through which the parasite enters. The fewer stomata there are, the fewer infections there will be, and the plant will appear correspondingly resistant.

VII. CONTROL

1. Laboratory Toxicity Tests.

In all the toxicological experiments, the general method was that of Reddick and Wallace (1910). The fungicides used in these toxicity tests were prepared by Dr. O. R. Butler. Glass slides were cleaned in potassium bichromate cleaning solution, rinsed in distilled water, and dried between filter papers. The solution, the toxicity of which was to be tested, was sprayed on the slide by means of an atomizer, and the slides were then dried. Fresh urediniospores were removed from living leaves by means of a stream of water from a pipette. These spores were shaken up in distilled water, drops of which were then placed on the sprayed and dried slides, and also on other unsprayed slides, used as checks. This gave conditions similar to those the spores meet on sprayed and unsprayed leaves. The spores were present in the drops in large enough numbers to be easily visible to the naked eye. The slides bearing the spores were then placed on culture plate benches in moist chambers, and these were placed at 100°, the optimum temperature for the germination of the urediniospores of Luccinia antirrhini. Here, they were allowed to remain for at least twelve hours, at the end of which time, the drops were examined, the spores counted, and the percentage of spores germinating were determined.

If there was no germination on the check (the unsprayed slides) the results on the sprayed slides were of course discarded. At least three tests were made with each strength of solution. Stronger and weaker solutions were used, but only dilutions near the limit of toxicity were given in the tables.

(a) Copper sulphate (

Tests were made with copper sulphate in dilutions ranging from .0039 per cent copper to .25 per cent copper. The toxicity of copper sulphate to the urediniospores is shown in the following table.

TABLE 7. Effect of Various Strengths of Copper Sulphate on the Germination of Uredospores.

Per cent Copper	Germination relative to Check - 100	Mean of three experiments				Remarks
.25	No germination					
.125	5	"	"	"	"	
.0625	5	"	"	"	"	
.0312	12	"	"	"	"	
.0159	18	"	"	"	"	
.0079	14	"	"	"	"	
.0039	24	"	"	"	"	

Copper sulphate prevents germination of the urediniospores of *L. antirrhini* at a strength of solution of .25% copper. Melhus (1915) found copper sulphate toxic to the spores of *Phytophthora infestans* when the solution contained .0157% copper. The Uredinales are evidently much more resistant to copper than are the Phycotomycetes.

Toxicity of Copper Sulphate to Foliage of Snapdragon.

The plants were sprayed with copper sulphate solutions containing from .25 to .0312% copper. The plants were dried slowly, that is they were allowed to remain six hours in a moist chamber after spraying.

TABLE 8. Toxicity of Copper Sulphate Spray to the Foliage of Snapdragon.

Per cent Copper	Injury to Foliage
.25	Markedly injured
.125	" "
.0625	Slightly injured
.0312	No injury

To prevent germination of urediniospores, the copper sulphate solution must contain .25% copper. But this amount of copper proves to be toxic to the foliage of the host. Copper sulphate cannot be used as control of snapdragon rust.

(c) Cuprammonium sulphate (*Eau celeste*)

Cuprammonium sulphate, $\text{Cu Sb}_4 \cdot 4 \text{ NH}_3 \cdot \text{H}_2\text{O}$, on drying gives rise to basic copper sulphate which on further weathering passes to copper sulphate. In these toxicity tests it was used in strengths of solution containing from 0.0312% to 0.50% copper sulphate.

TABLE 9. Effect of Various Strengths of Cuprammonium Sulphate on the Germination of the Uredospores.

Per cent Copper	Germination: Relative to Check = 100	Remarks
0.1300	No Germination	Mean of three experiments
0.0650	" "	" "
0.0325	4	" "
0.0162	22	" "
0.079	45	" "

A solution of cuprammonium sulphate containing .0625% copper prevents germination of urediniospores of *L. antirrhini*. The toxicity of this solution to the foliage of snapdragon was tested as in the case of copper sulphate. Solutions containing .25% and .125% copper injured the foliage markedly, and a solution containing .0625% copper produced slight injury. Cuprammonium sulphate at the strength toxic to the parasite is injurious to the host plant.

Other copper salts were not tested, for Melhus (1915) has

found cupric sulphate ($\text{Cu SO}_4 \cdot 5 \text{ H}_2\text{O}$); cupric nitrate ($\text{Cu } \text{NO}_3 \cdot \text{ H}_2\text{O}$); cupric acetate ($\text{Cu C}_2\text{H}_3\text{O}_2 \cdot \text{ H}_2\text{O}$); and cupric chloride ($\text{Cu Cl}_2 \cdot \text{ H}_2\text{O}$) to be about equally toxic if they contain the same amounts of the toxic principle, copper.

(d) Hammond's Copper Solution.

Hammond's Copper solution is a commercial preparation which has been used by florists in the attempt to control carnation rust. This stock solution was analysed by Dr. Smith, assistant chemist at the New Hampshire Experiment Station, and found to contain 0.0180 gms. copper in 1 cc. of solution. The makers recommend that it be applied at the rate of one quart of the stock solution to twenty-five gallons of water, that is in a solution containing .018% copper. Its toxicity at various strengths to the uredospores of Fusca antirrhini and of Uromyces Caryophyllinus was tested.

TABLE 10. Effect of Various Strengths of Hammond's Copper Solution on the Germination of the uredospores.

Strength of Solution. Per Cent Copper	Germination Relative to Check - 100	Remarks
0.18	5	Mean of three experiments
0.144	8	" " "
0.12	19	" " "
0.072	18	" " "
0.036	17	" two "
0.014	40	" three "
0.018	72	" " "

It is evident that Hammond's Copper Solution, even when used ten times the recommended strength, does not prevent germination of uredospores of F. antirrhini. Its action on carnation rust was also tested, and at the recommended strength it was not toxic, the germination of the uredospores of U. Caryophyllinus relative to check - 100, being 56.

(a) Bordeaux mixture.

The Bordeaux mixture used contained copper sulphate and calcium oxide in the approximate ratio of 1:0.3, that is, calcium oxide was added to slight alkalinity. This formula was used for the sake of convenience, but the same results would be obtained with any current formula, for the unit copper is equally toxic in acid, neutral, and alkaline Bordeaux mixtures (Butler, 1915). This Bordeaux mixture used in the tests was diluted to various strengths, so as to contain the following percentages of copper sulphate: .0156%, .0312%, .0625%, .125%, .25%, .50%, 1%, 2%, and 4%.

TABLE 11. Effect of Various Strengths of Bordeaux mixture, 1:0.3, on the Germination of the Uredospores of *L. antirrhini*.

Strength of Solution Per cent Copper Sulphate	Per cent Copper Sulphate	Germination Relative to Check - 100	Mean of three experiments	Remarks
4.00	1.00	24	"	
2.00	0.50	25	"	"
1.00	0.25	15	"	"
0.50	0.125	32	"	"
0.25	0.0625	33	"	"
0.125	0.0312	23	"	"
0.0625	0.0159	20	"	one
0.0312	0.0079	20	"	three
0.0156	0.0039	40	"	"

The urediniospores of *L. antirrhini* were able to germinate in all the strengths of Bordeaux mixture employed. They germinated as readily in the mixture containing 1% Cu. as in the mixture containing 0.0039% Cu. There was a 10% difference in favor of the weaker mixture, but this has no significance when we consider the irregular fluctuations shown by the intermediate strengths. It is probable that at the lesser strengths, the sprayed slide or leaf offers the maximum surface of solute to the solvent. An increased strength, as 1% copper, means that the particles on the slide or leaf merely overlap each other, and do not offer an increased surface proportional to the added amount of

substance. Having found a certain strength of Bordeaux mixture non-toxic to the uredospores, increasing the strength of the mixture results in no toxic effect.

To confirm the results of the toxicity tests of Bordeaux mixture against Luccinia antirrhini, snapdragon plants were sprayed with Bordeaux mixture 1:0.3 containing 1% copper sulphate. All the plants used in this experiment were of the same variety. These sprayed plants were allowed to dry, and then they and other plants not sprayed were inoculated with snapdragon rust, the spores being applied to the plant in distilled water by means of an atomizer. All inoculated plants, both sprayed and unsprayed, were then placed for twelve hours in an incubator at 10 degrees C. The plants were then placed together in a greenhouse under the same conditions. Fifteen days after inoculation, the sprayed and unsprayed plants which had been inoculated were examined and the uredosori breaking out through the leaves were counted. The sprayed plants showed, on the average, two hundred sori each, while the unsprayed plants showed on the average two hundred and ten sori each. That is, there was an approximately equal number of rust pustules on the sprayed and unsprayed plants. Snapdragon plants sprayed with Bordeaux mixture bear as much rust as those not sprayed, and Bordeaux mixture can not be recommended for the control of snapdragon rust.

Continuing the study of the toxicity of Bordeaux mixture to members of the Uredinales, the writer tested its effect on the germination of the uredospores of carnation rust, Uromyces caryophyllinus. It is realized that growers do not often spray for carnation rust now, being able to control this disease by cultural methods and varietal selection. But Bordeaux mixture has often been recommended for the control of carnation rust. Bordeaux mixture 1:0.3 was used in these

tests in various strengths so as to contain .5%, 1%, 2%, and 4% copper sulphate. The method employed was the same as that described for L. antirrhini, except that the spores were germinated at 14°C, the optimum germination temperature of the uredospores of L. Caryophyllinus. These uredospores, like those of L. antirrhini, germinated only when in contact with both air and water, spores in the interior of the drop of water never germinating.

Bordeaux mixture is not toxic to the spores of Uromyces Caryophyllinus which indicates that the behavior of the urediniospores of L. antirrhini toward this fungicide is not exceptional. If carnation plants sprayed with Bordeaux mixture failed to rust, it must have been due to other adverse conditions such as temperature, which prevented infection.

It would appear from data obtained by the investigators and also from results here reported that the Uredinales are much more tolerant of copper than are the Hycomycetes. Melhus (1915) found Bordeaux mixture toxic to Phytophthora infestans at .0039% copper sulphate, but the writer did not find Bordeaux mixture toxic to the two members of Uredinales studied at 4% copper sulphate. It may be that the thick wall of the spores of the Uredinales is the protection, or it may be that the spore secretes some chemical substance which prevents the copper in the Bordeaux mixture from going into solution.

(e) Miscellaneous.

The literature contains numerous references to the use of copper solutions as a control of diseases produced by members of the Uredinales. But there is a variance of opinion as to the effectiveness of copper as a control of rust diseases. The experiments performed by earlier investigators were mostly of the field rather than laboratory type. Kimsey (1897) sprayed carnations with Bordeaux

mixture, and concluded that this treatment did not control the rust. Bailey and Lodeman (1895) sprayed carnations with a mixture of Bordeaux mixture and soap. They also used a mixture of copper chloride, lime, and soap. They concluded that the copper fungicides were most efficient in the control of carnation rust. Stewart (1896) recommends spraying with weak copper sulphate, for the control of carnation rust. The same investigator found that the spores of carnation rust can germinate in a copper sulphate solution containing .025% copper and that they germinate slightly in copper sulphate solutions containing as much as .083% Cu. He found the spores unable to germinate in 1 to 3000 solution of potassium sulfide. He found that if copper sulphate was applied to cuttings in a solution strong enough to control the rust, the plants were injured. He found that Bordeaux mixture would not control carnation rust. He recommends spraying the carnations with a 0.56% copper sulphate solution or with a 0.78% solution of potassium sulphide, 1 oz. to 1 gal. water. Maynard (1893) found Bordeaux mixture to give very good results as a control of carnation rust. J. Stuart (1894) found that Bordeaux mixture of standard and half strength solutions gave the best results in the control of carnation rust. Abbey (1898) recommends Bordeaux mixture as an efficient fungicide in the control of chrysanthemum rust. Dudley (1890) recommended a saturated solution of potassium permanganate as a control of hollyhock rust. Sturgis (1896) also recommended potassium permanganate for the control of hollyhock rust. R. D. Halstead (1897) sprayed hollyhocks with Bordeaux mixture, and found rust on all the check plants, while but one sprayed section showed any rust. Fornel (1893) tried to control rusts on oats and wheat by spraying with Bordeaux mixture, but found

no appreciable difference in the amount of disease on the sprayed and unsprayed plants. Hitchcock and Darleton (1893) found the spores of Luccinia graminis able to germinate in thirty chemical compounds of various strengths. They found these spores unable to germinate in a 0.1% solution of the following: mercuric chloride, copper acetate, potassium bichromate, potassium cyanide, acetic acid, and sulphuric acid.

A survey of the literature on rust control by fungicides is not very helpful. Some of the statements made are misleading and few are very convincing. For instance, it is hard to see how potassium permanganate could be of any great value in combatting a rust. Potassium permanganate destroys organisms by oxidizing them, and if in contact with oxidizable material, it very soon loses its power, and would hence be of no avail against spores which subsequently fall upon the sprayed surface. Some investigators found Bordeaux mixture efficient and some found it inefficient as a fungicide for the control of rust. The narrow range of temperature in which the spores can germinate may have been exceeded, and the credit for no spores germinating may have been given to the fungicide instead of to a temperature above the optimum, which, as we have seen, reduces or prevents germination. But the literature cited indicates that the rusts are very resistant to copper solutions and to fungicides in general.

(g) Sulphur.

Dusting with sulphur has been used successfully for several years as a control of Luccinia asparagi in California. Butler (1917) was the first to describe a sulphur dust control for rust of snapdragons. The toxicity of sulphur applied in water instead of

as a dust was first tested. Powdered sulphur, washed and freed of $S O_2$, was added to drops of distilled water in which urediniospores of *P. entirrhini* were placed. These spores in water with sulphur and spores in water without sulphur were then placed at a temperature of 10°C. Subsequent examination showed that the spores in water with sulphur germinated quite as well as the spores in water without sulphur.

TABLE 12. Effect of Sulphur in water on the Germination of the Uredospores.

Germination Relative to Check - 100	Remarks
100.5	*mean of five experiments

This result is not surprising, for sulphur being insoluble would hardly be expected to have a fungicidal effect when applied in water. This result agrees with that of Melhus (1915) who found that the spores of *Phytophthora infestans* germinated as easily in water containing sulphur as in pure water.

Toxicity of Dry Sulphur to Urediniospores of *Fuccinia entirrhini*

Dry urediniospores were placed on slides and dusted with powdered sulphur. These were then placed in dessicators and placed for three and one-half hours, some at a temperature of 12 degrees C. and some at a temperature of 21 degrees C. These dry spores which had been sulphured at the two different temperatures were then placed in drops of distilled water, and set away for twelve hours at their optimum temperature for germination, 10 degrees C. They were accompanied by unsulphured spores as checks. The following table shows the relative germination of the spores, including those not sulphured, those sulphured at 12 degrees C., and those sulphured at 21 degrees C.

TABLE 13. Effect of Dry Sulphur and its Temperature of Application on the Germination of the Uredospores.

Germination of Spores exposed to Sulphur Relative to Check - 100		Remarks
21°C	120°F	
0	90.1	Mean of ten experiments

Spores dusted with powdered sulphur and kept for 3½ hours at a temperature of 21 degrees C. (70 degrees F.) do not germinate. Spores similarly treated but kept during the sulphuring at a lower temperature, 12 degrees C. (53.6 degrees F.), germinate as well as unsulphured spores. Sulphur at the lower temperature is comparatively inert. But at the higher temperature, it reacts slowly with the oxygen of the air to form sulphur dioxide.

The previous experiment showed that sulphur as such is not toxic to the spores of this fungus. It is rather the sulphur dioxide generated by the exposure of dry sulphur to warm air that is toxic to the spores of the fungus. The more surface a substance exposes, the more rapidly it reacts chemically. Hence the necessity of having finely divided, that is, finely powdered, sulphur rather than coarser grade.

As a continuation of this experiment, urediniospores were taken from snapdragon plants which had been dusted with powdered sulphur at a temperature not less than 70 degrees F. These plants bore many spore pustules, and the fungus was to all appearances vigorous. But these spores refused to germinate when placed under optimum conditions for germination. The results are expressed in the following table.

TABLE 14. Germination of Urediniospores taken from sulphured plants.

Germination Relative to Check - 100	
Spores from Sulphured Plants	Spores from unsulphured Plants
0	100

(g) Fungine

Fungine is a commercial preparation which has been used by some growers in their attempts to control snapdragon rust. As stated by the makers, it contains potassium polysulfide 6%, and potassium thiosulphate 4%. The writer tested the toxicity of this preparation to the spores of Uromyces Caryophyllinus and of Luccinia antirrhini. At the various strengths tested and at the strength recommended by the makers, Fungine proved toxic to the spores of both of these fungi.

TABLE 15. Effect of Various Strengths of Fungine on the Germination of the Uredospores of *L. antirrhini* and of *U. Caryophyllinus*.

Strength of Solution	Germination relative to Check - 100		Remarks			
Per cent Thiosulfate	<i>P. antirrhini</i>	<i>U. Caryophyllinus</i>	Mean of 4 experiments	"	"	"
0.25	0	0	"	"	"	"
0.50	0	0	"	"	"	"
1.0	0	0	"	"	"	"

Fungine, though toxic to the spores of these fungi, has certain disadvantages. It is no more efficient than powdered sulphur, but it costs more than the sulphur, until the sulphur dust reaches parts of the plant which a liquid spray could not. Fungine when sprayed on a slide or leaf has a physical character resembling a soap film, and this soapiness makes it wash off the leaf too easily.

2. Temperature Regulation.

It has been shown that the uredospores of *Uuccinia* *antirrhini* cannot germinate below 5°c. nor above 20°c., and that they germinate best at 10°c or 50°F. 50°F is the night temperature at which the snapdragon is usually grown under glass; it is frequently grown in the house with curritions. This temperature results in a maximum amount of rust on the snapdragon. The currition, on the other hand, is grown at a night temperature of 4°C. below its optimum for germination, and this may in part explain why currition rust is so much less serious than snapdragon rust. Day temperatures of the houses are not important in the study of snapdragon rust, for those temperatures are always too high for germination of the uredospores, so we may consider infection as taking place only in the night. If growers would raise or lower the night temperature of the snapdragon house to 52°F or 48°F, the rust would decrease in amount about 50%. This is shown in the constant curve showing the relation between temperature and germination. It must be remembered that this temperature change prevents infection and prevents the spread of the disease, but it does not kill the spores. So if the temperature approaches the germination optimum even for a few hours, the disease may break out again. Rise of temperature as a control is further considered under treatment with sulphur. Growers may object to raising the temperature very much above 50°F because of the danger of shortening the blossom spikes, but a rise of even 2° or 3° will check the rust, and is not likely to diminish the value of the blossom spikes.

3. Selection of Resistant Varieties.

Forty-seven varieties of snapdragon have been observed by

the writer and their relative resistance to *Uuccinia antirrhini* has been determined. The most susceptible varieties are Half Dwarf, Rose Queen, Ruby, Carter's Link, Delicate Rose, Half Dwarf Golden Queen, Fiery Belt, Bridesmaid, Crimson Queen Victoria, Sulphur Yellow, Venus, Carter's Gold Crest, and Chamois. It is recommended that the above varieties be not grown at all. The most resistant varieties are Queen of the North, Pure White, Rose Dore, Giant White, Crimson, Giant Blood Red, Giant Yellow, Striped Varieties, Hephaestos, Phelps White, White Queen Victoria, Firebrand, and Pont Blanc. It is recommended that outdoor gardeners confine themselves principally to these varieties. These varieties, while not absolutely resistant, are the nearest approach to it among snapdragons. Florists grow only a few varieties as a rule, notably Keystone, Silver Link, Buxton's Phelps White, and Nelrose. None of those varieties are resistant but Mr. A. B. Shaw (1917) of New Bedford, Massachusetts, writes that Keystone is slightly resistant. Florists can control this disease less by the selection of resistant varieties than can outdoor gardeners, but it is recommended that the florist propagate from resistant individuals and meanwhile safeguard his crop by the sulphur treatment.

4. Regulation of Moisture.

It has been shown that although temperature does not kill the uredospores of *U. antirrhini*, six weeks of drying does kill them. The teliospore may be eliminated, and as the urediniospores cannot germinate after six weeks of drying, there is no danger of the disease being transmitted on dry seed. Also, it is evidently impossible for urediniospores to live from season to season in a greenhouse if the snapdragons are removed and the house deprived of water for a period of at least eight weeks. A case of this kind has recently come to

the attention of the writer. A house of snapdragons was severely attacked by rust last year. This year, mignonette is being grown in the space occupied by last year's rusted snapdragons. Among the mignonette plants are many seedling snapdragons, the descendants of the rusted plants. But these seedlings are absolutely clean and free from rust. Here, we have a case of seed from infected plants producing seedlings free from the disease, although they are growing in the space occupied by the diseased plants the previous year.

Apparently, their only protection is the laying out of the urediniospores.

5. Use of Fungicides

The copper salts and copper mixtures, the toxicity of which to Fuccinia antirrhini were tested, are copper sulphate, cuprammonium sulphate (Eau celeste), Bordeaux mixture (cupric sulphate to calcium oxide in the ratio of 1 to 0.3 present) and Hammond's Copper solution. It was shown that Bordeaux mixture is absolutely useless for the control of this disease, for at no strength suitable for use on plants does it prevent germination, and sprayed plants when inoculated develop quite as much rust as plants similarly inoculated but not sprayed. The toxic constituent of Bordeaux mixture is copper sulphate, and this used alone has a toxic effect on the spores of Fuccinia antirrhini, but in Bordeaux mixture this toxic constituent or active principle does not dissolve sufficiently rapidly to be efficient against either Fuccinia antirrhini or Uromyces laryophyllinus.

Copper sulphate solution, .25% copper, is toxic to the urediniospores of L. antirrhini. But the use of this strength of copper sulphate on snapdragon is precluded because of its toxic effect on the foliage. Cuprammonium sulphate (Eau celeste) is toxic

to the urediniospores of *P. antirrhini* at .0625% copper. But this strength of hau celeste is liable to result in a toxic action to the foliage of snapdragon, unless the foliage can dry off in less than one hour. This nearly precludes the use of hau celeste on thick crowded plants, for the bottom foliage would dry off too slowly. Hau celeste can be used only when the principle toxic to the foliage can be volatilized by rapid drying. Hammond's Copper solution is not toxic to the urediniospores of *P. antirrhini*, and is therefore of no use for the control of snapdragon rust.

(a) Dusting

A method for the control of snapdragon rust by dusting the plants with sulphur has been described by Dr. O. A. Buttr (1917). During the past winter (1916-1917) the writer has inspected, at intervals of two weeks, greenhouses of snapdragon which had been thus treated. When the treatment began, the plants were in very bad shape. Leaves and stems were fairly covered with rust pustules. The first thing done was to cut out those shoots so badly infected as to be hopeless; many of them were girdled and dying. The sulphur used was obtained from the Union Sulphur Co., and from the Corona Chemical Co. It is powdered finely enough to pass through a sieve having 40,000 holes to the square inch. It was applied with a good bellows that filled the air of the greenhouse with dust, which settled as a thin, even film on the foliage. For plants ten inches high, 4 ounces of sulphur were applied to 150 square feet of bench. The sulphuring was repeated at intervals of two to three weeks, as necessitated by new growth of the plants. Exposed blossoms were injured but there was no injury to the leaves. For two days after sulphuring, the night temperature

was kept between 60 and 70 degrees F. Spores from these sulphured plants were tested from time to time and were uniformly unable to germinate. The mycelium in the plant remained alive, and occasionally produced new sori near the old ones. But new infections were impossible, and the spread of the disease was checked. In one case, some young plants which had been sulphured became infected but the explanation was soon found. They had been grown since sulphuring at a temperature not over 50 degrees F. To be successful, the sulphur must be accompanied by some rise in temperature.

(b) Spraying with Polysulphides.

Fungine, a potassium polysulfide preparation is toxic to the uredospores of I. antirrhini. It controls snapdragon rust, if applied to the plant frequently, but its use is not recommended for it has no advantages over powdered sulphur, while it costs more, and cannot be applied as thoroughly as can a dust.

6. Review of Control Measures

Many of the experiments already described contain suggestions as to the control of snapdragon rust. They may be summed up as follows:

1. There is only very slight chance of rust entering a house of the seeds. The uredospores would not live on the seeds. Teliospores are not formed till after seed is harvested, and are of no use to the fungus when formed.

2. A house which has contained snapdragon rust should not be used for snapdragons the following year if any plants have remained alive during the interim, nor unless the house has been dried out.

3. Cuttings should not be taken from a bench showing rust. If such cuttings must be used, dust them with powdered sulphur, and give them a high temperature a few nights.

4. Select varieties showing resistance to rust. The list of varieties showing relative susceptibility should be of assistance here.

5. Keep water off snapdragon foliage. In watering, wet only the soil. If syringing becomes necessary, do it on a sunny morning so that the foliage will dry off quickly.

6. Keep the insects down; they serve to spread the rust. But cyanide must be used carefully, as snapdragons are easily injured by it.

7. Dust the plants with finely powdered sulphur, if rust appears. If only a few isolated leaves are infected remove them by hand picking. Apply the sulphur with a good bellows that will throw clouds of dust. Keep the temperature up for a few nights. (For more detail on sulphuring, see the article by Dr. O. R. Butler, 1917).

8. If spraying is to be done, remember Bordeaux mixture is of no use. A solution of cuproammonium sulphate containing .0625% salt will control the fungus. But because of its toxic effect on the foliage, it can be used with safety only when the sprayed foliage will dry off within one hour.

9. If rust appears, run the temperature up to 60 degrees F. at night for a few nights, till the rust has been placed under control of sulphuring or hand-picking. Remember 50 degrees F. is the temperature most favorable to the fungus.

VIII. SUMMARY

Uuccinia antirrhini Diet & Holw. is known to occur only on *Antirrhinum majus*.

Rust is the most serious disease of snapdragons under glass, and is second in importance to anthracnose on snapdragons out of doors.

The urediniospores germinate moderately well with an optimum temperature of 10°C.; the teliospores have not been germinated.

Dry urediniospores do not retain the power of germination more than six weeks.

No varieties of snapdragon are absolutely resistant to the parasite, but some are relatively resistant. The varietal resistance is dependent on the relative number of stomata per unit area of leaf surface.

The urediniospores are disseminated by cuttings, insects, water, and wind.

A solution of Copper sulphate is toxic to the urediniospores of *U. antirrhini*.

A solution of .25% cuprammonium sulphate is toxic to the urediniospores of *U. antirrhini*.

Bordeaux mixture is not toxic to the urediniospores of *U. antirrhini*.

The SO₂ generated by dry sulphur at a temperature of 21°C. is toxic to the urediniospores of *U. antirrhini*.

The method of control recommended consists in growing resistant varieties, controlling cultural conditions carefully, dusting with powdered sulphur at a temperature of 70°F., and keeping the night temperature of the snapdragon house above 52°F. or below 48°F.



1



2



3

Plate I

Figures 1 & 2. Infected Leaves

Figure 3. Infected Plant.

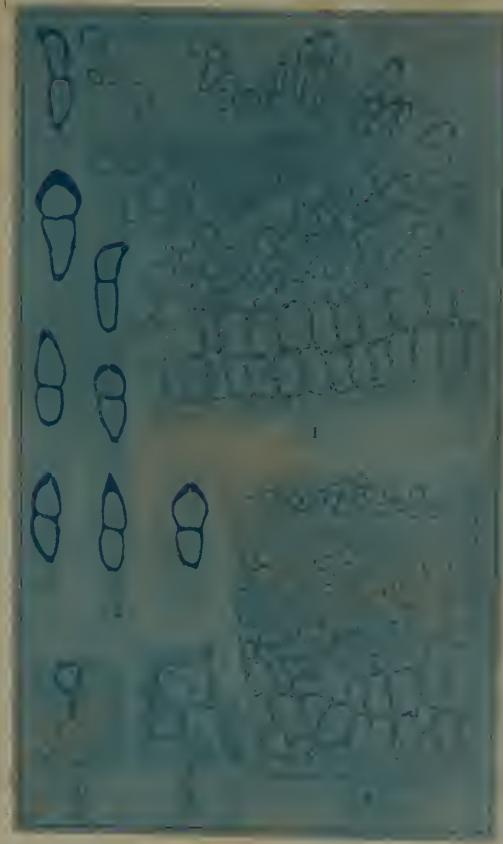


Plate 2.

Figure 1. Cross Section of Telium
Figure 2. Types of Teliospores
Figure 3, a, b, d, etc. Germ Tube entering Stoma
Figure 4. Haustoria
Figure 5. Cross Section of Uredinium

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